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# Griffing and Hayman Diallel Analyses of Variance for Eating and Processing Quality Parameters of Milled Rice[1]

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**Abstract** : Amylose content and amylographic viscosity measurements, both chemical and physical properties of milled rice, are important eating and processing quality parameters and are characteristics of a endosperm. A six-parent diallel cross was made and, thus, a genetic study on such endosperm characteristics was conducted. Since amylose contern and amylographic viscosity measurements are difficult to be determined on a single grain basis, samples of bulking heterozygous $F_2$ grains from combining homogeneous heterozygous $F_1$ plants were used as measurement units. Results of Griffing's and Hayman's diallel analyses of variance for the parameters, amylose content and amylographic peak, hot-paste, cool-paste , breakdown, setback and consistency viscosities, are respectively presented. It was evident that gene action in the parents studied was mainly additive for all evaluated endosperm characteristics, although dominance effects were also involved. The fact that reciprocal differences in both Griffing's and Hayman's diallel analyses were not significant indicated that Hayman's assumption (2) no differences between reciprocal crosses was met in this study. Date indicated that significant dominance gene effects wer due to a directional dominance effect, an asymmetry of the gene distribution, and a residual dominance effect for all studied quality parameters except for hot-paste viscosity, in which the effect of an asymmetry of the gene distribution was not significant.

Key words : Amylose content, Amylographic viscosity measurements, Diallel analysis, Endosperm characteristics, Milled rice.

## INTRODUCTION

Amylose content and amylographic viscosity measurements of milled rice, considered mainly as eating and processing quality parameters, are characteristics of the endosperm, which is a triploid tissue resulting from the fusion of one sperm nucleus with the two polar nuclei of the egg. Thus, reciprocal differences (including maternal and/or dosage effects, xenia) are supposedly existed and the grains on a plant of segregating generations represent the next generation of the plant. Furthermore, for endosperm characteristics, an individual is a

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seed, not a plant. That is, these characteristics should be measured on a single grain basis. Unfortunately, there are many endosperm characteristics which are difficult to measure on the basis of single seed and a satisfactory genetic model for such endosperm characteristics has not yet been developed. Up to present, a method for determining amylose content on the basis of single grain has already been developed and few papers has paid attention to solve the lack of proper genetic models for those endosperm characteristics[23,24,25,28]. However, determination of amylographic viscosity measurements has not been developed yet. All seeds on a plant have to be taken as a measurement unit. On the other hand, a diallel cross which consists of mating several parental entries in all possible combinations, allows a genetic analysis to be carried out after one generation and may provide a large simple size of measurement unit for endosperm characteristic by combining all $F_2$ grains from some homogeneous heterozygous $F_1$ plants. Thus, using the first filial generation with the parents and requiring fewer individuals, genetic and beeding information about endosperm characterisitics can be obtained[16].

Up to now, several methods have been proposed for the analysis of data from a diallel cross [6,7,9,10,12]. Liu[19], Mather and Poysa [21], and Sokol and Baker[26] have demonstrated basic similarity of these methods. The approaches of Griffing[6] (Method I, Model I) and Hayman [9,10] are statistically similar, In their analyses of variance, the Griffing's general combining ability (GCA) component is mathematically identical to the Hayman's additive component(a). Griffing employs one specific combining ability (SCA) and one reciprocal effect component, while Hayman subdivides these into three dominance components ($b_1$, $b_2$, and $b_3$), and two reciprocal effect components (c and d), respectively. They differ, however, in the genetic assumptions and interpretations which are associated with them. The Griffing's analysis is a strictly statistical treatment of main effects (GCA) and interactions (SCA), whereas, the Hayman analysis incorporates genetic assumptions. In general, the Hayman's method appears to extract mor genetic information than the Griffing's method does from the same data set. The Griffing's method involves only analysis of variance and estimation of GCA and SCA effects. The Hayman's method, on the other hand, may include statistical and graphical analyses of array variances and covariances, and the estimation of a number of genetic parameters.

In this paper, data about amylose content and amylographic viscosity measurements, based upon determination of combining $F_2$ milled rice grains, were analyzed by both the Griffing and the Hayman diallel analyses of variance and the genetic control about those quality parameters of rice are discussed.

## MATERIALS AND METHODS

All possible cross-combinations, including the reciprocals, were made among six rice entries, "Rexmont", "Guichow", "Lemont", "Cl 9902", "Toro 11", and "Taichung Sen No. 10" (TCS 10), representing an array of different levels of amylose content and amylographic measurements as shown in Fig. 1 and Table 1. The six parents and one set of $F_1$ hybrids, 30 combinations, were transplanted and cultivated in a flooded paddy field at the Texas A&M University Agricultural Research and Extension Center near Beaumont, Texas, in a randomized complete block design with three replications. Each block consisted of 36 four-row plots. Each plot included 40 plants spaced at 30×30 cm. Twenty plants from the two central rows of each plot were harvested and analyzed.

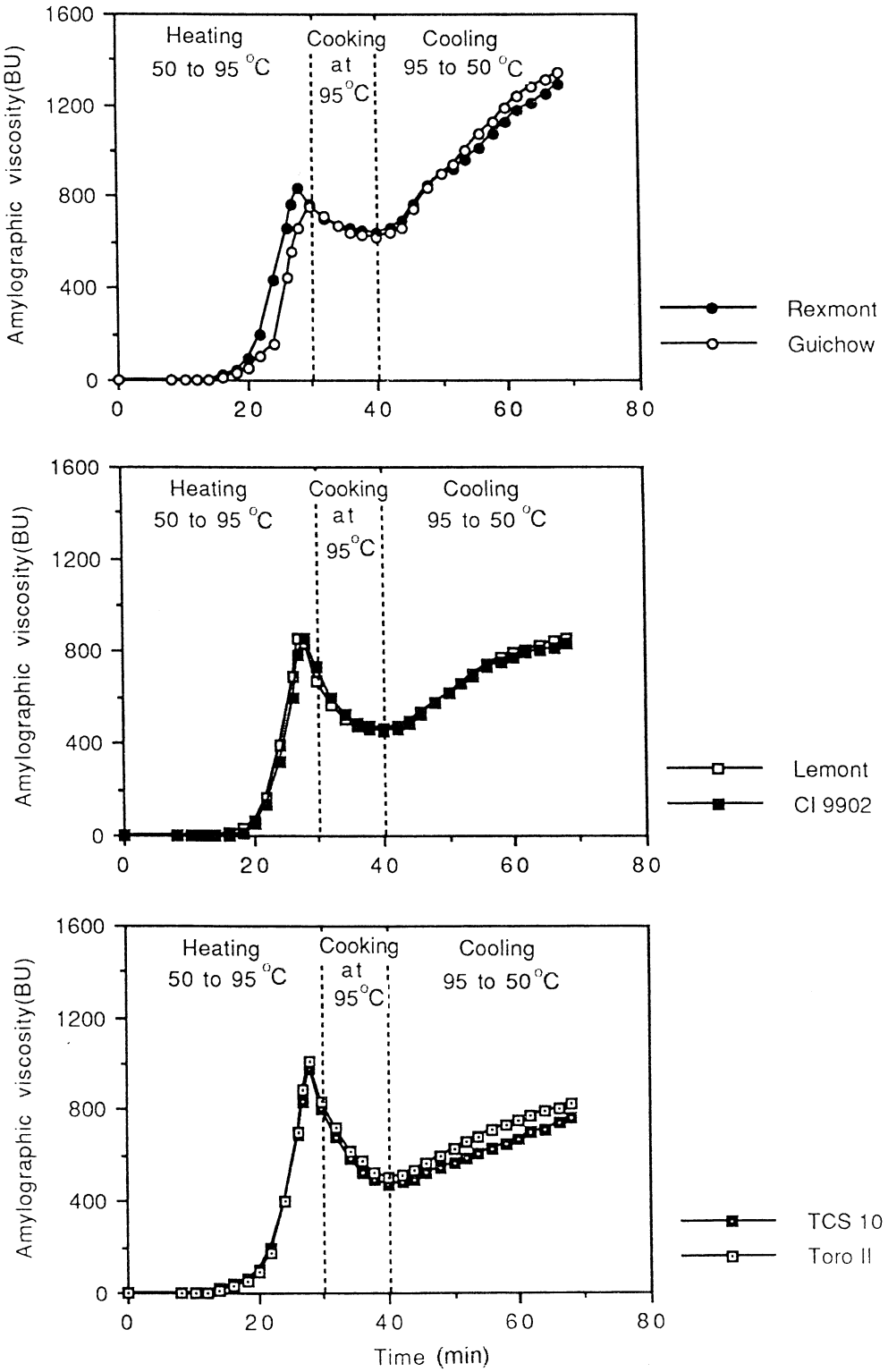


Fig. 1. Amylographic profiles of the six parents used in the diallel cross.

Table 1. Means values of amylose content and amylographic viscosity measurements of the six rice parental entries.

| Parent | Amylose content (%) | Amylographic viscosity(BU)[z] | | | | | |
|---|---|---|---|---|---|---|---|
| | | Peak | Hot-paste | Cool-paste | Breakdown | Setback | Consistency |
| Rexmont(P1) | 26.3 | 833 | 640 | 1,290 | 193 | 457 | 650 |
| Guichow(P2) | 27.4 | 747 | 620 | 1,340 | 127 | 593 | 720 |
| Lemont(P3) | 22.3 | 843 | 463 | 857 | 380 | 13 | 393 |
| Cl 9902(P4) | 22.6 | 853 | 470 | 843 | 383 | − 10 | 373 |
| TCS 10(P5) | 14.5 | 997 | 490 | 757 | 507 | −240 | 267 |
| Toro ll(P6) | 15.2 | 1,010 | 510 | 803 | 500 | −207 | 293 |

[z] Brabender Unit.

Amylose content of milled rice was analyzed by a totally automated system of amylose analysis in white milled rice innovated by Webb[28]. Amylographic pasting characteristics were determined by the method developed by Halick and Kelly[8] and further modified for use at the Regional Rice Quality Laboratory, USDA, Beaumont, Texas, using a Brabender Visco/Amylograph with 700g.cm sensitivity cartridge and 75 rpm speed (C. W. Brabender Instruments Inc., S. Hackensack, NJ). The detailed procedure had been outlined in previous paper[17].

The Griffing (method I, Model I) and Hayman diallel analyses of variance were performed based upon the original models and assumptions[6,7,9,10]. In each analysis of variance, the "a" item is an estimate of genetic variation among parents; the "b" item is an estimate of dominance variance sat some of the loci; the $b_1$ item is an estimate of mean dominance deviation of the $F_1$'s from their mid-parent values; the $b_2$ item is an estimate of the mean dominance deviation of the $F_1$ from their mid-parental values within each array differing over arrays; the $b_3$item is an estimate of residual dominance effect; the "c" item detects the average maternal effects of each parental line; and the "d" item detects the reciprocal difference not ascribable to "c".

## RESULTS

Traditional analyses of variance for characteristics studied had revealed highly significant differences among treatments (parents and hybrids)(Table 2), indicating the presence of genotypic variability in these populations used. Further detailed analyses of variance of the diallel on quality parameters were, therefore, performed and presented as the following.

Table 2. Analysis of variance for amylose content and amylographic viscosity measurements of rice.

| SOV | DF | Mean square | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Amylose | Peak | Hot-past | Cool-paste | Breakdown | Setback | Consistency |
| Block | 2 | 0.8 | 485.8 | 398.5 | 156.8 | 164.2 | 260.0 | 65.1 |
| Treatment | 35 | 13.7** | 7,440.7** | 2,770.7** | 29,283.0** | 13,219.4** | 54,799.4** | 15,347.8** |
| Error | 70 | 0.26 | 191.5 | 90.9 | 293.6 | 139.4 | 215.1 | 98.1 |

** Significant at the 0.01 probability level.

### Percent Amylose Content

The analyses of variance of the diallel table for amylose content followed by both Griffing's and Hayman's methods were presented in Table 3. The results of the significance tests for both Griffing's and Hayman's methods, as shown in Table 3, were the same. This provided a practical numerical instance to certify that both Griffing's and Hayman's analyses are statistically similar.

Table 3. Griffing and Hayman analyses of variance of amylose content in the six-parent diallel crosses of rice.

| Griffing | | | Hayman | | |
|---|---|---|---|---|---|
| SOV | DF | Mean square | SOV | DF | Mean square |
| GCA | 5 | 78.87** | a | 5 | 78.87** |
| SCA | 15 | 5.43** | b | 15 | 5.43** |
| | | | $b_1$ | 1 | 24.67** |
| | | | $b_2$ | 5 | 1.06** |
| | | | $b_3$ | 9 | 5.72** |
| Reciprocal | 15 | 0.28 | c | 5 | 0.12 |
| | | | d | 10 | 0.36 |
| Error | 70 | 0.26 | Error | 70 | 0.26 |

** significant at the 0.01 probability level.

Heghly significant differences from the zero were observed for both GCA and SCA in Griffing's method and both items "a" and "b" in Hayman's method, respectively. The reciprocal component in Griffing's method and both items "c" and "d" in Hayman's method were not significantly different from zero. Furthermore, the mean squares for both GCA and "a" were significantly larger than those for both SCA and "b" for amylose content. According to Mather and Jinks[20], the "a" item primarily tests the significance of the additive effects of the gene, and the "b" item the dominance effects. Yates[35], on the other hand, described that such a GCA may be sometimes called "additive genetic component" or"main effect", while a SCA may be referred to as "non-additive genetic component" or "dominance component" or "interaction effect". Therefore, data shown in Table 3 indicated that the inheritance of amylose content was controlled largely by additive gene effects, although dominance gene effects were also involved. No reciprocal effect influencing amylose content was indicated.

The "$b_1$" item tests the mean deviation of the $F_1$s from their mid-parental values. it is significant only if the dominance deviations of the genes in the various entries used are predominantly in one direction. That it, there is a directional dominance effect. The "$b_2$" item tests whether the mean dominance deviation of the $F_1$s from their mid-parental values within each array differs over arrays. It will do so if some parents contain considerably more dominant alleles than others. That is, a significant "$b_2$" implies asymmetry of the gene distribution in the parents at the loci exhibiting dominance. The "$b_3$" item tests that part of

the dominance that is unique to each $F_1$[20]. Thus, the information from Table 3 indicated that the significant dominance effects (b) were due to a directional dominance erffect ($b_1$), an asymmetry of the gene distribution ($b_2$), and a residual dominance effect ($b_3$) coming from additive× additive, additive×dominance, and additive×dominance interaction effects that are not attributed to $b_1$ and $b_2$.

From the results reported here, it can be concluded that : (1)gene action in these genotypes used was mainly additive for milled rice amylose content, although dominance effects were also involved; (2) the significant dominance gene effects were due to a directional dominance effect, an asymmetry of the gene distribution, and a residual dominance effect; (3) reciprocal differences due to cytoplasmic and/or dosage, xenia effects, upon amylose content were not found;

### Amylographic Peak Viscosity

There are three basic amylographic viscosity measurements: amylographic peak viscosi -ty, hot-paste viscosity, and cool-paste viscosity. From which, amylographic breakdown viscosity, setback viscosity, and consistency viscosity can be calculated. Amylographic peak viscosity is the viscosity when a aqueous suspension of starch of a given concentration is heated. Usually, peak viscosity occurs before or after the temperature of the suspension has reached to 92-95 °C. Amylographic peak viscosity is a measurement of the ability of the known starch granules to swell markedly before rupturing. Typical U. S. long-grain rice cultivars usually showed an intermediate peak viscosity[29,31,32,33]. Scientists in Japan and in Taiwan, ROC. found that sticky cooked rice has higher amylographic peak viscosity[18,27]. Thus, amylographic peak viscosity is an important index for evaluating rice grain quality.

The analyses of variance of the diallel table for both Griffing's and Hayman's methods for amylographic hot-paste viscosity were presented in Tables 4. Highly significant differences were observed for both additive gene effects (GCA and "a") and dominance gene effects (SCA and "b"), and no significant differences were found for reciprocal (maternal) component. Since the mean square ratio of additive gene effect mean squares to dominance gene effect mean squares was 6:1, it can be concluded that the inheritance of amylographic peak viscosity was controlled by both additive and dominance genes, with the additive gene effects being larger than dominance gene effects. The significant dominance effects were due to a directional dominance effect ($b_1$), and imbalance of gene distribution ($b_2$), and a residual dominance effect ($b_3$) resulted from additive × additive, additive × dominance, and dominance × dominance interaction effects.

From the information shown in Tables 4, it might indicate that: (1)gene action in these crosses was largely additive for amylographic peak viscosity although dominance gene effects were also involved; (2) the significant dominance gene effects were due to a directional dominance effect, an asymmetry of the gene distribution, and a residual dominance effect; (3) reciprocal differences were not detected in this characteristic;

Table 4. Griffing and Hayman analyses of variance of amylgraphic peak viscosity in the six-parent diallel crosses of rice.

| Griffing | | | Hayman | | |
|---|---|---|---|---|---|
| SOV | DF | Mean square | SOV | DF | Mean square |
| GCA | 5 | 34,234.32** | a | 5 | 34,234.32** |
| SCA | 15 | 5,725.39** | b | 15 | 5,725.39** |
| | | | $b_1$ | 1 | 8,634.32** |
| | | | $b_2$ | 5 | 5,985.86** |
| | | | $b_3$ | 9 | 5,257.47** |
| Reciprocal | 15 | 224.81 | c | 5 | 87.41 |
| | | | d | 10 | 293.52 |
| Error | 70 | 191.53 | Error | 70 | 191.53 |

** significant at the 0.01 probability level.

### Amylographic Hot-paste Viscosity

Amylographic hot-paste viscosity is measured as the paste is cooking at a specified high temperature (usually 92-95 °C) for 10 minutes. The overall relationship between amylographic hot-paste viscosity and grain quality is not clear, although Lii et al.[18] reported that amylographic hot-paste viscosity significantly positively correlated with eating quality.

Tests for significance on both Griffing's and Hayman's diallel analyses for amylographic hot-paste viscosity, presented in Table 5, were the same. Highly significantly differences from the zero were found for both additive gene effects (GCA and "a") and dominance gene effects (SCA and "b"). However, the mean squares for GCA and "a" were very much larger than those for SCA and "b" and the mean square ratio of additive gene effects to dominance gene effects was 45:1. These data suggested the although both additive gene effects and dominance gene effects influenced the phenotypic mean for amylographic hot-paste viscosity in the parent entries used, the inheritance of this characteristic was mainly controlled by additive gene effects. No significant differences were observied for reciprocal components, indicating that maternal effects upon amylographic hot-paste viscosity can be ignored in these genotypes used. The data from the analysis according to Hayman's method further indicated that the significant dominance effects (b) for this characteristic were due to a directional dominance effect ($b_1$), and dominance that is unique to each $F_1$($b_3$).

From these results, one could conclude that: (1) gene action in these crosses was principally additive for amylographic hot-paste viscosity, although there were some dominance gene effects; (2) the significant dominance gene effects were due to a directional dominance effect and a residual dominance effect only; (3) reciprocal differences were insignificant.

Table 5. Griffing and Hayman analyses of variance of amylgraphic hot-paste viscosity in the six-parent diallel crosses of rice.

| Griffing | | | Hayman | | |
|---|---|---|---|---|---|
| SOV | DF | Mean square | SOV | DF | Mean square |
| GCA | 5 | 17,905.80** | a | 5 | 17,905.80** |
| SCA | 15 | 395.95** | b | 15 | 395.95** |
| | | | $b_1$ | 1 | 437.10** |
| | | | $b_2$ | 5 | 168.09** |
| | | | $b_3$ | 9 | 555.00** |
| Reciprocal | 15 | 100.37 | c | 5 | 140.00 |
| | | | d | 10 | 80.56 |
| Error | 70 | 90.84 | Error | 70 | 90.84 |

** significant at the 0.01 probability level.

### Amylographic Cool-paste Viscosity

Amylographic cool-paste viscosity is measured as the temperature of the paste is cooled down at a certain rate (usually 1.5 °Cmin.) to 50 °C after a holding period (usually 10 minutes) at a spectified high temperature (usually 92-95 °C). Typical U. S. medium-and short-grain cultivars show a comparatively low cool-paste viscosity[29,31,32,33]. In addition, a higher amylographic cool-paste viscosity combined with lower amylographic breakdown viscosity has been correlated with superior parboil-canning characteristics and quick-cooking properties [34].

Griffing's and Hayman's diallel analyses of variance for amylographic cool-paste viscosity (Table 6), indicated that the results of the significance test for both methods were the same. Highly significant differences were observed for both additive gene effects (GCA and "a") and dominance gene effects (SCA and "b"). Besides, the mean squares for GCA and "a" were much larger than those for SCA and "b" and the mean square ratio of additive gene effevts to dominance gene effects was 58:1, indicating that the inheritance of amylographic cool-paste viscosity was mainly controlled by additive gene effects even though dominance gene effects are also involved. No significant differences were found for reciprocal (maternal) components. Analysis of Hayman's method further indicated that the significant dominance effects were due to an asymmetry of the gene distribution ($b_2$), and a residual dominance effect ($b_3$). A non-significant value of $b_1$ shows that dominance gene effects for the characteristics are ambidirectional dominance[20]. That is, the increasing (or decreasing) genes are dominant in some parents, but sometimes are recessive in some of the other parents.

From these results, it could be concluded that: (1) gene action in these crosses is mainly additive for amylographic cool-paste viscosity, although dominance gene effects are also involved; (2) reciprocal effects might not be present; (3) the significant dominance gene effects are due to an asymmetry of the gene distribution, and a residual dominance effect;

Table 6. Griffing and Hayman analyses of variance of amylgraphic cool-paste viscosity in the six-parent diallel crosses of rice.

| Griffing | | | Hayman | | |
|---|---|---|---|---|---|
| SOV | DF | Mean square | SOV | DF | Mean square |
| GCA | 5 | 193,822.10** | a | 5 | 193,822.10** |
| SCA | 15 | 3,332.67** | b | 15 | 3,332.67** |
| | | | $b_1$ | 1 | 723.21** |
| | | | $b_2$ | 5 | 1,086.05** |
| | | | $b_3$ | 9 | 3,537.41** |
| Reciprocal | 15 | 387.04 | c | 5 | 603.70 |
| | | | d | 10 | 383.70 |
| Error | 70 | 293.62 | Error | 70 | 293.62 |

** significant at the 0.01 probability level.

### Amylographic Breakdown Viscosity

There are three derivative amylographic viscosity measurements: amylograhic breakdown viscosity, setback viscosity, and consistency viscosity. Amylographic breakdown viscosity is calculated from amylographic decrease in viscosity during cooking at 92-95°C.

Traditional U. S. long-, medium-, and short-grain rice cultivars show relatively high amylographic breakdown viscosity. In contrast, superior cooking and processing U. S. long-grain cultivars are characterized by an amylose content 2-4% higher than those of typical U. S. long-grain cultivars and a relatively low amylographic breakdown viscosity[2,3,30,32,34]. Japanese rice scientists suggested that amylographic breakdown viscosity could be selected as an index feactor for palatability evaluation[27]. Published results from Taiwan, ROC. suggested a highly significant correlation between amylographic breakdown viscosity and eating quality[18]. Amylographic breakdown viscosity, therefore, could be considered as the most important index for evaluating grain quality among all of the six amylographic viscosity measurements.

The analyses of variance of the diallel tables for both Griffing's and Hayman's methods for amylographic breakdown viscosity were enumerated together in Table 7. The results of tests for significance for both methods of analyses were the same. Highly significant differences for both additive gene effects (GCA and "a") and dominance gene effects (SCA and "b") were observed. The mean square ratio of additive gene effects to dominance gene effects was 17: 1, suggesting that the inheritance of amylographic breakdown viscosity was controlled mainly by additive, although dominance gene effects were also involved. No significant differences were found for reciprocal components, indicating that reciprocal effects upon amylographic breakdown viscosity might not have existed among the genotypes used. In addition, the adta from the analysis of Hayman's method further indicated that the significant dominance gene effects were due to a directional dominance effect ($b_1$), an asymmetry of the gene distribution ($b_2$), and a residual dominance effect ($b_3$), which are part of the dominance deviation that is unique to each $F_1$ not attributable to

$b_1$ and $b_2$[20].

The results submitted here might suggest that: (1) gene action for amylographic breakdown viscosity in these crosses was mainly additive, although dominance gene effects were also presented; (2) reciprocal effects were not found; (3) the significant dominance gene effects were due to a directional dominance effect, an asymmetry of the gene distribution, and a residual dominance effect.

Table 7. Griffing and Hayman analyses of variance of amylographic breakdown viscosity in the six-parent diallel crosses of rice.

| Griffing | | | Hayman | | |
|---|---|---|---|---|---|
| SOV | DF | Mean square | SOV | DF | Mean square |
| GCA | 5 | 78,325.06** | a | 5 | 78,325.06** |
| SCA | 15 | 4,616.81** | b | 15 | 4,616.81** |
| | | | $b_1$ | 1 | 10,631.17** |
| | | | $b_2$ | 5 | 4,773.09** |
| | | | $b_3$ | 9 | 3,861.73** |
| Reciprocal | 15 | 120.00 | c | 5 | 34.81 |
| | | | d | 10 | 162.59 |
| Error | 70 | 139.43 | Error | 70 | 139.43 |

** significant at the 0.01 probability level.

### Amylographic Setback Viscosity

Amylographic setback viscosity is a derivative amylographic viscosity measurement calculated from amylographic cool-paste viscosity minus amylographic peak viscosity. Traditional southern U. S. long-grain cultivare show a slightly positive amylographic estback viscosity. Superior cooking and processing U. S. long-grain cultivars, on the other hand, show a higher amylographic setback viscosity[2,3,30,32,34]. Thus, amylographic setback viscosity is an important inde for evaluating grain quality although more attention has traditionally been paid to amylose content and amylographic breakdown viscosity.

The results of the tests for significance for both Griffing's and Hayman's for amylographic setback viscosity were the same (Table 8). Highly significant differences for both additive gene effects (GCA and "a") and dominance gene effects (SCA and "b") were observed. It was clear that the mean squares for both GCA and "a" were significantly larger that those for both SCA and "b" and the mean square ratio of additive gene effects to dominance gene effects was 32:1. These data indicated that though the inheritance of amylographic setback viscosity was controlled mainly by additive gene effects, dominance gene effects were still involved. No significant differences in reciprocal components were detected, suggesting that reciprocal effects upon amylographic setback viscosity did not exist among these entries used. data from Hayman's diallel analysis also implied that the significant dominance gene effects were due to a directional dominance effect ($b_1$), an asymmetry of the gene distribution ($b_2$), and a residual dominance ($b_3$).

From the results described here, it might indicate that: (1) gene action in these crosses was mainly additive for amylographic setback viscosity, although dominance gene effects were also involved; (2) the significant dominance gene effects were due to a directional dominance effect, an asymmetry dominance of the gene distribution, and a residual dominance effect; (3) reciprocal effects were not found.

Table 8. Griffing and Hayman analyses of variance of amylographic setback viscosity in the six-parent diallel crosses of rice.

| Griffing | | | Hayman | | |
|---|---|---|---|---|---|
| SOV | DF | Mean square | SOV | DF | Mean square |
| GCA | 5 | 350,065.93** | a | 5 | 350,065.93** |
| SCA | 15 | 10,863.95** | b | 15 | 10,863.95** |
| | | | $b_1$ | 1 | 42,320.00** |
| | | | $b_2$ | 5 | 7,464.07** |
| | | | $b_3$ | 9 | 9,257.65** |
| Reciprocal | 15 | 312.59 | c | 5 | 186.67 |
| | | | d | 10 | 375.56 |
| Error | 70 | 215.05 | Error | 70 | 215.05 |

** significant at the 0.01 probability level.

### Amylographic Consistency Viscosity

Amylographic consistency viscosity is one of the derivative viscosity measurements calculated by subtracting amylographic hot-paste viscosity from amylographic cool-paste viscosity. Up to now, less attention has been paid to this characteristic.

The results of the tests for significance for both Griffing's and Hayman's diallel analyses for amylographic consistency viscosity, enumerated in Table 9. were principally the same. Highly significant differences were found for additive gene effects (GCA and "a") and dominance gene effects (SCA and "b"). Furthermore, the mean squares for both GCA and "a" were much larger that those for both SCA and "b". The mean square ratio of additive gene effects to dominance gene effects was 46:1, implying that the inheritnce if amylographic consistency viscosity was controlled largely by additive gene effects, plus some dominance gene effects. In addition, the information form the analysis according to Hayman's method indicated that the significant dominance gene effects were due to a directional dominance effect ($b_1$), an asymmetry of the gene distribution ($b_2$), and a residual dominance ($b_3$). No significant differences were observed for reciprocal components, suggesting that resiprocal effects upon amylographic consistency viscosity might be ignored.

From the results presented here, a sub-conclusion could be offered that: (1) gene action in these crosses was mainly additive for amylographic consistency viscosity, although dominance gene effects were also present; (2) the significant dominance gene effects were due to a directional dominance effect, an asymmetry of the gene distribution, and a residual dominance effect; (3) reciprocal differences were not detected.

Table 9. Griffing and Hayman analyses of variance of amylographic consistency viscosity in the six-parent diallel crosses of rice.

| Griffing | | | Hayman | | |
|---|---|---|---|---|---|
| SOV | DF | Mean square | SOV | DF | Mean square |
| GCA | 5 | 100,342.84** | a | 5 | 100,342.84** |
| SCA | 15 | 2,191.38** | b | 15 | 2,191.38** |
| | | | $b_1$ | 1 | 10,528.95** |
| | | | $b_2$ | 5 | 721.23** |
| | | | $b_3$ | 9 | 2,081.73** |
| Reciprocal | 15 | 172.59 | c | 5 | 137.04 |
| | | | d | 10 | 190.37 |
| Error | 70 | 98.14 | Error | 70 | 98.14 |

** significant at the 0.01 probability level.

## DISCUSSION

Although a diallel cross experiment provides a powerful method of investigating the genetic properties of a group of homozygous genotypes, the analysis of a diallel cross has suffered from several theoretical defects. That is, the genetic interpretation of the data from diallel experiments is valid only if certain assumption about the parental materials are true [9,10]. The genetic assumptions, postulated by Hayman[9,10] are: (1) diploid segregation; (2) no differences between reciprocal crosses; (3) independent action of non-allelic genes; (4) no multiple allelism; (5) homozygous parents; and (6) independent distribution of genes in the parents. Of these assumptions, some can be accepted more easily than others. From a genetic point of view, two assumptions, independent distribution of genes in the parents and independent action non-allelic genes, are biologically unrealistic in attempts to interpret the results of diallel analyses. The assumption concerning independent distribution of genes in the parents is most unrealistic to proper interpretation and seems to be least acceptable in actual practice. The assumption dealing with independent action of non-allelic genes, i. e., no epistasis, may frequently be unjustifiable[1,5,26].

The assumption of independent distribution of genes in the parents implies that the presence or absence of an allele at a particular locus is statistically independent of the presence or absence of an allele at any other locus. Thus, it seems that assuming genes are independently distributed in the parents of a dialle cross is not realistic. Failure of this assumption may result from, linkage of genes in the population from which the parents were chosen, or from the effects of sample size when sampling the parents[1]. From a review of the literature, Baker[1] pointed out that there is general agreement that failure of this assumption will often result in overestimation of the average level of dominance. However, there are conflicting reports as to whether or not failure of this assumption will result in biased estimates of general and specific combining ability components of variance. Gilert[5] suggestd that the assumption of independent action of non-allelic genes (no epistasis)

cannot be justified from our knowledge of biochemical pathways on plants. He concluded that such an assumption can only be justified on an empirical basis. Hayman[10] outlined a test for the presence of epistasis based on his graphical analysis of data from diallel crosses. However, reports showed that Hayman's test for epistasis is reliable only if genes are distributed independently in the parents of the diallel. Matzinger and Kempthorne[22] reported that estimate of general combining ability (GCA) variance includes primarily additive genetic variance and portions of epistatic variances and estimate of specific combining ability (SCA) variances includes dominance genetic variance and portions of the various types of epistatic variances when epistatic effects are present in the diallel cross experiment. Thus, the estimates of GCA and SCA are unbiased only if the diallel cross experiment is in the absence of epistasis.

Form a statistical point of view, the concern is the choice of a model with either fixed or random genotypic effects. Griffing[6] developed his analyses in terms of both fixed and random models and suggested that the choice of the correct model depended on the nature of parental materials. Gardner and Eberhart[4] stated that plant breeders and geneticists were usually interested in genetic information about a particular set of parents and should, generally, be using a fixed model in most cases. Hayman[11], in discussing the number of parents required in diallel experiments, concluded that estimates of components of variation could not be reliable estimataes of population parameters unless the number of parents exceeds 10. However, with fewer parents, a fixed model is recommended. In this case, the individual parents and crosses are the main interest, and not a reference population. That is, a large scale diallel cross would use a model with random genotypic effects, a small diallel cross, on the other hand, requires a fixed model.

Form a plant breeding point of view, Gilbert[5] gave a critical evaluation of the diallel cross technique. He concluded that in practical breeding work, its utility to breeders may be exaggerated and information obtained does not appear to be directly relevant to practical breeding work. On the other hand, Johnson[14], through analysis of diallel graph from barley breeding data, argued tdhat compared to other methods available, the diallel cross technique provided a more systematic approach to meet large-scale studies of quantitative characteristics. His results indicated that reliable genetic information could be obtained on dominance and recessiveness, and additional information of the genetic identity of evaluated characteristics in genotypes used would give invaluable guidance to plant breeders

Despite criticism of these assumptions as being unjustifiable and biologically unrealistic [1,5,26] and arguments as to the practical benefit for probems of breeders[5,14], breeders and geneticists continue to use Hayman's diallel analysis. This is probably due to a paucity of alternative methods for obtaining genetic information on quantitative characteristics[1,21,26].

In the presents study, the assumption of homozygous parents was definitely assured because rice is a self-pollinated crop and parental entries used were all pure line cultivars. Although the characteristics studied were all endosperm characteristics which are under triploid genetic control, the gene behavior for these characteristics during meiosis is followed of diploid segregation principle. Thus, the assumption of diploid segregation was met.

The remaining four assumptions have not so easily been justified. Due to expression of endosperm characteristics is under triploid genetic control, the reciprocal differences ( including maternal and/or dosage effects, xenia) of these evaluated characteristics were supposedly existed. However, the results obtained from the analysis of variance of diallel tables indicated that no definite evidences for reciprocal differences of these evaluated characteristics were observed. However, the results might be biased by bulking $F_2$ grains.

The genetic model obtained from the analysis of variance of the diallel tables indicated that the assumptions of independent distribution of genes in the parents and independent action of non-allelic genes appeard to have failed for the endosperm characteristics studied. According to Baker[1], failure of the assumption of independent distribution of genes in the parents may result from linkage of genes in the population from which the parents were chosen or from the effects of sample size when sampling the parents. In the present diallel experiment, six rice entries, Rexmont, Guichow, Lemont, Cl 9902, Toro II, and TCS 10, representing three distinct endosperm types, were used as the parents. Rexmont, representing the first major improvement in the U. S. long-grain quality, was developed specifically to satisfy the rice industry's need, and is the forerunner of rice of superior cooking and processing quality. The distinguishing quality characteristics of Rexmont are amylose content 2-4% higher than traditional southern U. S. long-grain cultivars combined with a lower amylographic breakdown viscosity. Guichow, a Chinese *indica* cultivar with high amylose content and low amylographic breakdown viscosity, is a typical short-grain cultivar released from China mainland under a breeding program with high yielding as a priority. Lemont, a leading cultivar in southern rice producing states, represents a high quality traditional southern U. S. Long-grain cultivar, Toro II was a specialty rice produced in limited amount for local markets. Toro II consumers like its clingy cooked texture. TCS 10 also a high yielding *indica* cultivar was released from a Taiwan, ROC. breeding program in 1975 with a high yielding and high quality (in particular low amylose level) as priorities. Generally, Toro II and TCS 10 have a grain size and shape similar to that of the U. S. long -grain type, but cooking and eating behavior similar to those of the U. S. short-and medium -grain types. As Webb and Stermer[34] mentioned, historically and now through planned breeding, specific milling, cooking, eating, and processing characteristics are associated with each grain type of the U. S. rice cultivars. However, this association of grain type with rice quality characteristics definitely not existed in the entries used as parents in this six-parent rice diallel cross. Therefore, among these parents, it might be inferred that the presence or absence of an allele conditioning the endosperm characteristics studied at a particular locus is statistically and genetically independent of the presence or absence of an allele at any other locus. That is, in the present diallel experiment, if the failure of the assumption, independent distribution of genes in the parents, is justified, it should mainly result from the effects of sample size when sampling the parents, as followed by the standpoint of Baker[1].

In addition, Kumar and Khush[15] argued that analyses of genetically heterozygous bulk seed samples on plants provided biased information for the genetic study on endosperm

characteristics, such as amylose content. In this study, genetically heterozygous $F_2$ bulk grain samples on homogeneous heterozygous, $F_1$ plants were run for amylose content and amylographic viscosity measurements. This might be another issue in this paper and had to be kept in mind.

In conclusion, compared with other plant quantitative characteristics such as plant height, panicle length, etc., endosperm characteristics differ in three distinct ways, as mentioned above. The lack of both proper genetic model and analysis technology has been an obstacle in studying the genetic behavior of endosperm characteristics. Therefore, establishing a quantitative genetic model and developing a analysis technique based on single grain basis for endosperm characteristics will be of benefit to breeding programs in cereal crops that high grain quality is a priority.

## REFERENCES

1. Baker, R. J. 1978. Issues in diallel analysis. Crop Sci. 18: 533—536.
2. Bollich, C. N., B. D. Webb, M. A. Marchetti, and J. E. Scott. 1980. Registration of Newrex rice. Crop Sci. 20: 285—286.
3. Bollich, C. N., B. D. Webb, and J. E. Scott. 1979. Rice breeding in the Southern United States. pp. 303—323. In: Bilogy and Breeding for Resistance to Arthropods and Pathogens in Agriculture Plants. M. K. Harris ed. Texas Agric. Exp. Stn., College Station, TX.
4. Gardner, C. O., and S. A. Eberhart. 1966. Analysis and interpretation of the variety cross diallel and related population. Biometrics 22: 439—452.
5. Gibert, N. E. G. 1958. Diallel cross in plant breeding. Heredity 12: 477—492.
6. Griffing, B. 1956a. Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. 9: 463—493.
7. Griffing, B. 1956b. A generalized treatment of the use of diallel crosses in quantitative inheritance. Heredity 10: 31—50.
8. Halick, J. V., and V. J. Kelly. 1959. Gelatinization and pasting characteristics of rice varieties as related to cooking behavior. Cereal Chem. 36: 91—98.
9. Hayman, B. I. 1954a. The analysis of variance of diallel tables. Biometrics 10: 235—244.
10. Hayman, B. I. 1954b. The theory and analysis of diallel crosses. Genetics 39: 789—809.
11. Hayman, B. I. 1963. Notes on diallel cross theory. pp. 571—578. In: Statistical Genetics and Plant Breeding. NAS-NRC-892.
12. Jinks, J. L. 1954. The analysis of continuous variation in a diallel cross of Nicotina rustica varieties. Geneticsl 39: 767—788.
13. Jinks, J. L. 1956. The $F_2$ and backcross generations from a set of diallel crosses. Heredity 10: 1—30.
14. Johnson, L. P. V. 1963. Applications of the diallel-cross techniques to plant breeding. pp. 561—570. In: Statistical Genetics and Plant Breeding. NAS—NRC-982.
15. Kumar, I., and G. S. Khush. 1987. Genetic analysis of different amylose levels in rice. Crop Sci. 27: 1167—1172.
16. Kuo. Y. C., 1992. Genetic analyses of eating and processing quality parameters in rice (*Oryza sativa* L.). Ph. D. Diss., Texas A&M Univ., TX., 163pp.
17. Kuo, Y. C., B. D. Webb, and J. W. Stansel. 1996. Genetic analysis of amylographic viscosity measurements of milled rice by means of diallel graph. J. Agric. Res. China 45 : 319—335.
18. Lii, C. Y., S. M. Chang, and H. L. Yang. 1986. Correlation between the physico-chemical propetries and

the eating quality of milled rice in Taiwan. Bull. Inst. chem. Academia Sinica. 33: 55—62.

19. Liu, C. 1986. Component analysis of heterozygous diallel crosses. J. Agric. Res. China. 33: 475—483.
20. Mather, K., and J. L. Jinks. 1971. Biometrical Genetics. Cornell Univ. Press, Ithaca, NY, USA, 282pp.
21. Mather, D. E., and V. W. Poysa. 1983. Griffeng and Hayman diallel analyses of protein and lysine content of spring triticale. Can. J. Genet. Cytol. 25: 384—389.
22. Matzinger, D. F., and O. Kempthorne. 1956. The modified diallel table with partial inbreeding and interactions with environment. Genetics 41: 822—833.
23. Mo, H. D. 1988. Genetic expression for endsperm traits. pp. 478—487. In: Proceedings of the Second International Conference on Quantitative Genetics. B. S. Weir, E. J. Eisen, M. M. Goodman, and G. Namkoong ed. sinauer Assoc. Inc., Sunderland, MA.
24. Pooni, H. S., I Kumar, G. S. Khush. 1991. A comprehensive model for disomically inherited metrical traits expressed in triploid tissues. Heredity 69: 166—174.
25. Pooni, H. S., I Kumar, G. S. Khush. 1992. Genetical control of amylose content in selected crosses of *indica* rice. Heredity 70: 269—280.
26. Sokol, M. L., and R. J. Baker. 1977. Evaluation of the assumptions required for the genetic interpretation of diallel experiments in self-pollinating crop. Can. J. Plant Sci. 57: 1185—1191.
27. Suzuki, H. 1979. Amylography and alkali viscosigraphy of rice. pp. 261—282. In: Proc. Workshop on Chemical Aspects of Rice Grain Quality. Int. Rice Res. Inst., Los Banos, Philippines.
28. Webb, B. D. 1972. A totally automated procedure for amylose analysis in whole kermel milled rice. pp. 62—63. In: Proc. 14th Rice Tech. Working Groups. Univ. of Calif. Davis. CA.
29. Webb, B. D. 1975. Cooking, processing, and milling qualities of rice. pp. 97—106. In: Six Decades of Rice Research in Texas. Texas Agric. Exp. Stn. College Station, TX.
30. Webb, B. D. 1980. Rice quality and grades. pp. 543—565. In: Rice: Production and Utilization. B. S. Luh ed. AVI Publ, Co., Inc., Westport, CT.
31. Webb, B. D. 1985. Criteria of rice quality in the United Stataes. pp. 403—442. In: Rice: Chemistry and Technology. 2nd ed., B. O. Juliano ed Am. Assoc. Cereal Chem. St. Paul., MN.
32. Webb, B. D., C. N. Bollich, H. L. Carnahan, K. A. Kuenzel, and S. M. McKenzie. 1985. Utilization characteristics and qualities of United States rice. pp. 25—35. In: Rice Grain Quality and Marketing. Int. Rice Rex. Inst., Los Banos, Philippines.
33. Webb, B. D., C. N. Bollich, N. E. Jodon, T. H. Johnston, and D. H. Bowman. 1972. Evaluating the milling, cooking, and processing characteristics required of rice vareties in the United States. USDA, ARS-S-1, Washington, D. C.
34. Webb, B. D., and R. A. Stermer. 1972. Criteria of rice quality. pp. 102—139. In: Rice: Chemistry and Tecnology. lst ed., D. F. Houston ed., Am. Assoc. Cereal Chem. St. Paul, MN.
35. Yates, F. 1947. Analysis of data from all possible reciprocal crosses between a set of parental lines. Heredity 1: 287—301.

# 白米食用與加工品質性狀之 Griffing 與 Hayman 氏全互交變方分析[1]

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**摘要**：直鏈澱粉含量與澱粉黏度測定值爲白米主要之化學與物理特性，更是稻米食用與加工品質之重要指標性狀，屬胚乳性狀。本研究利用水稻六親本全互交以進行該等性狀之遺傳分析。由於直鏈澱粉含量與澱粉糊黏度測定值之測定無法以單粒法進行，本研究以混合同組合諸遺傳異質 $F_1$ 稻株所得諸遺傳異質 $F_2$ 米粒爲供測樣品，數據經以 Griffing 與 Hayman 兩套方法分析，並按直鏈澱粉含量、澱粉糊高峰黏度、熱糊黏度、冷糊黏度、崩解黏度、回饋黏度與膠體黏度等分別討論。數據顯示七個品質性狀之顯性效應雖存在，但主要受累加性基因所控制。Griffing 與 Hayman 兩套分析顯示七個品質性狀正反交差異均不顯著之事實指出，本研究參試親本符合 Hayman 氏正反交無差異之第二前題。受測各品質性狀之顯性效應除熱糊黏度外，均肇因於單向顯性、基因分布未勻稱所呈之顯性與殘餘顯性等三成份，而熱糊黏度之三類顯性成份中，基因分布未勻稱所呈之顯性值未具統計意義。

**關鍵詞**：直鏈澱粉含量、澱粉糊黏度測定值、全互交分析、胚乳性狀、白米。

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